RESEARCH ARTICLE

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Distribution of carangid larvae (Teleostei: Carangidae) and concentrations of zooplankton in the northern Gulf of Mexico, with illustrations of early *Hemicaranx amblyrhynchus* and *Caranx* spp. larvae

Abstract We examined 1,825 bongo-net samples collected during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of United States Gulf of Mexico waters (1982–1986) for carangid larvae. Objectives were to describe the distribution of carangid larvae and to examine distribution patterns relative to areas of higher zooplankton volumes in order to reveal areas that may be important nurseries. Samples contained about 29,200 carangid larvae from 13 species or species complexes in 11 genera. *Chloroscombrus chrysurus* and *Decapterus punctatus* accounted for 91.7% of all larvae. We found that the 'scads' (*D. punctatus*, *Trachurus lathami*, and *Selar crumenophthalmus*) utilize temporally and/or spatially distinct spawning strategies to reduce co-occurrence of larvae. Samples contained fewer larvae than expected of the amberjacks (*Seriola* spp.), *Caranx crysos*, and *C. hippos/latus* given the abundance of adults in the survey area, possibly due to inadequate sampling at appropriate times and locations, gear avoidance, or gear bias. Zooplankton displacement volumes (ZDVs) differed among regions and seasons and were inversely related to surface salinity and station depth. Differences among years were not significant. ZDVs were consistently highest near the Mississippi River delta and along the western Louisiana/eastern Texas shelf, and moderately high during summer and fall along the shelf break, with localized pockets of elevated volumes over the eastern Gulf shelf. We suggest that *Chloroscombrus chrysurus*, *D. punctatus*, *T. lathami*, and possibly *Oligoplites saurus*, *Hemicaranx amblyrhynchus* and *Caranx crysos* spawn in frontal areas and/or along other hydrographic features that promote higher productivity. We provide new illustrations and descriptive information for the larvae of *H. amblyrhynchus* and discuss characters that separate early larvae of several species of *Caranx*.

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Introduction

Members of the family Carangidae represent about 5% of the world's annual marine finfish landings, with major fisheries concentrating primarily on *Decapterus punctatus* (round scad) and *Trachurus lathami* (rough scad) (Leak 1977). Although Nakamura (1980) reported 24 species of carangids in the northern Gulf of Mexico (Gulf), information on the distribution and abundance of most carangids is inadequate to determine the feasibility of exploitation or greater exploitation. Exploratory surveys of the Gulf report potentially commercial quantities of adult *D. punctatus*, *T. lathami*, *Caranx crysos* (blue runner), and *Chloroscombrus chrysurus* (Atlantic bumper), but only *D. punctatus* are presently exploited (Juhl 1966; Bullis and Carpenter 1968; Bullis and Thompson 1970; Klima 1971). The small but abundant *C. chrysurus* may serve as an important food for predatory game and commercially important fishes (Reintjes 1979) and has value for reduction to fishmeal and fish oil (Leak 1977). Other carangids are highly regarded as food (pompano, *Trachinotus* spp.), game fish (*Elagatis bipinnulata*, rainbow runner; *Seriola* spp., amberjack), or bait (*Caranx crysos*, *D. punctatus*). Further, the amberjacks (*Seriola* spp.) currently face over-exploitation because of a dramatic increase in landings and the demand for fresh fish (Richards and McGowan 1989).

The distribution of carangid larvae in the Gulf is poorly known, with past studies focusing primarily on select taxa (Montolio 1976; Lyons 1978) or surveys of limited geographic and temporal coverage (Aprieto 1974; Houde et al. 1979; Leak 1981; Flores-Coto and Sanchez-Ramirez 1989; Sanchez-Ramirez and Flores-Coto 1993; Sanchez-Velasco and Flores-Coto 1994). A better understanding of spawning areas and seasonal spawning migrations requires basic information on the distribution of larvae, which is suggestive of the proximity of adult spawning concentrations (Houde 1982). Given that some fisheries exploit only spawning aggregations (Elwertowski and Boely 1971), a better understanding of the spatial and temporal distributions of carangid larvae may hasten development of fisheries (Leak 1981), permit better planning and development of ichthyoplankton surveys for spawning biomass estimation, and promote new fishery regulations for proper management of both new and existing fisheries. Our objectives were to describe the distribution of carangid larvae from United States Gulf of Mexico waters (an area that approximates the United States Exclusive Economic Zone/Fishery Conservation Zone), and to examine the distribution patterns of carangid larvae relative to areas of higher zooplankton volumes in order to reveal areas that may be important nurseries.

Material and methods

We examined 1,825 bongo-net samples for carangid larvae collected during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of United States Gulf of Mexico waters (i.e., the northern Gulf) from 1982 through 1986 (Fig. 1). National Marine Fisheries Service (NMFS) vessels sampled waters more than 10 m deep in a systematic grid of stations at about 55-km intervals. Coastal waters less than 10 m deep were sampled by participating Gulf States based on their sampling grid design. Texas did not participate.

Cruise survey procedures and zooplankton 'wet' volume displacement methods followed those outlined by Smith and Richardson (1977). Briefly, tows were made with a 60-cm bongo net (0.333-mm mesh) hauled-obliquely from within 5 m of the bottom or from a maximum depth of 200 m. A flowmeter mounted in the mouth of each net estimated the volume of water filtered. Ship speed was about 45 m/min and net retrieval was 20 m/min. Tows extended a minimum of 10 min in clear water or 5 min if waters were turbid and stations were less than 95 m deep. Time of the tow (day/night) depended on when the ship occupied a station. Differences between the number of bongo-net samples displaced to estimate zooplankton displacement volumes (ZDV) ($n = 1,664$) and the number of collections examined for fish larvae ($n = 1,825$) result from missing data. Zooplankton samples were strained by sieve to remove large coelenterates and non-planktonic organisms larger than 2.5 cm, displaced, and sorted for fish larvae. We standardized resulting ZDV to ml/100 m^3 and natural-log transformed values before statistical analyses. Standard SEAMAP sampling protocol fixed samples in 10% buffered formalin followed by a transfer to 70% ethyl alcohol after 48 h.
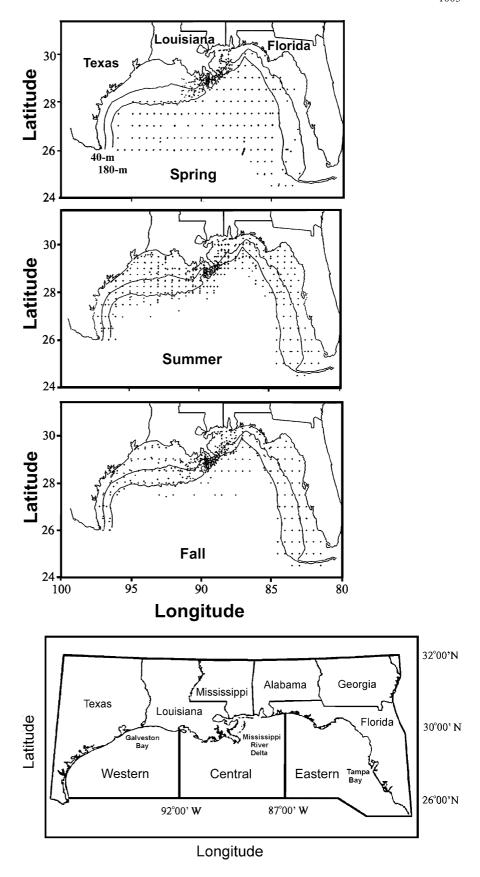
We based larval identifications on existing descriptive literature (i.e., Aprieto 1974; Laroche et. al. 1984), where possible, and our own descriptive work. We did not separate larvae smaller than 5 mm standard length (SL) of jack crevalle (*Caranx hippos*) from those of horse-eye jack (*C. latus*), or yellow jack [*C. (Carangoides)bartholomaei*] from those of bar jack [*C. (Carangoides) ruber*] because early larvae of these species have not been adequately described. Instead, we grouped these species into complexes (*C. hippos/latus* or *C. bartholomaei/ruber*). In addition, current descriptions of small *Seriola* and *Trachinotus* larvae are insufficient to permit reliable species separation and we discuss these at the generic level. We considered SL synonymous with notochord length in preflexion larvae and recorded all measurements as mm SL. We excluded carangids larger than 13.9 mm from analyses because bongo nets do not efficiently sample larger sizes.

Annual SEAMAP ichthyoplankton surveys did not sample all regions, months, and depth zones uniformly. Consequently, we do not compare inter-annual variability because of substantial differences in the temporal and spatial distributions of stations. Instead, we calculated a density (number of larvae/100 m^3) for each station and an arithmetic mean density for each month and region-season combination. We summed densities across stations within each category (i.e., month, season, depth, region, etc.) and divided the sum by the total number of stations in that category. Month was summed across years because not all months and regions were uniformly sampled over the study period.

We divided the northern Gulf into three geographic regions and three depth zones to examine carangid and zooplankton distribution patterns. Station depth served as a surrogate for distance from shore and the declining productivity gradient from the more eutrophic coastal waters to the oligotrophic open gulf waters. Inner continental shelf waters were less than 40 m deep; outer shelf waters were from 40 m to 180 m deep; and oceanic waters were those more than 180 m deep (Fig. 1). Differences among water masses, intensity of upwelling, and proximity to sources of freshwater and nutrient input can affect distribution and abundance patterns of zooplankton and fish larvae (Houde and Chitty 1976). The 40 m isobath, however, divided the continental shelf into areas of comparable size, which was convenient for evaluating differences in abundance between the inner and outer continental shelf. Latitude 24° 30′ N was the southern boundary of the survey area in the eastern Gulf and 26° 00′ N the southern boundary in the central and western Gulf (Fig. 1).

Hydrographic data were collected at the sea surface primarily by bucket. Water temperature was taken with

Fig. 1 Stations sampled during Southeast Assessment and Monitoring Program bongo-net surveys of the northern Gulf of Mexico (1982 through 1986) and defined areas

a hand-held thermometer and a water sample was returned to the laboratory for salinity analysis. We weighted hydrographic data by the number of larvae collected at each station before calculating the median and mean for each parameter, a method that emphasized the distribution of larvae rather than equally weighting stations. We are aware, however, that surface water temperature and salinity may be poor correlates of larval distribution patterns for those species not concentrated near the surface (Houde et al. 1979). Consequently, we used a percent cumulative frequency of 75% to define the hydrographic conditions (water temperature, salinity, and station depth) most often associated with the occurrence of larvae.

We grouped 3-month intervals into seasons based on monthly average water temperatures in the survey area as follows: Spring (March–May), Summer (June–August), Fall (September–November), and Winter (December–February). Cruises during April and May sampled primarily oceanic waters beyond the shelf in conjunction with NMFS annual larval tuna surveys. Cruises during March and from June through November sampled waters primarily over or immediately adjacent to the continental shelf (Fig. 1). We excluded winter from analyses, except in compiling hydrographic information for *Trachurus lathami*, because sampling was restricted primarily to waters near the Mississippi River delta in December.

Distribution and abundance patterns of carangid larvae permit inferences about adult distributions, spawning areas, and spawning times (Houde 1982). Accordingly, we compared the frequency distribution of stations where larvae were collected (positive catch stations) among regions, seasons, depth zones, and diel periods, respectively, with a likelihood ratio chi-square [$G^2, \alpha = 0.05$ (Daniel 1990)] and evaluated significant differences through contrasts. The original model included season, region, depth zone, and diel period as factors. We retested the model after excluding diel and all three-way interactions, which had a minimal effect on the model. We used a non-parametric Wilcoxon signed-ranks test to assess the significance of diel differences in density of larvae [$\alpha = 0.05$ (Daniel 1990)] and canonical correlation to assess the relationship between density of larvae, ZDV, and environmental variables. We considered relationships 'strong' if correlations were greater than 0.70, 'moderately strong' if greater than 0.60, 'significant' if greater than 0.50, and 'weak' if less than 0.50. We ran the canonical analyses on all stations sampled for the season(s) and region(s) of peak abundance, which was species-specific. We used ArcView GIS 3.1 software, a kriging function, linear semi-variogram, and the ordinary Gaussian method to generate ZDV plots. Cell size was 2 km and had a fixed radius. An average of the five nearest neighbors provided the cell mean. We used a nonparametric Friedman test (Daniel 1990) to examine differences in ZDV among seasons, regions, and depth zones. A Tukey's multiple range test established the significance of distribution patterns.

Table 1 Monthly mean density of carangid larvae (number of larvae/100 m³) for all stations sampled during SEAMAP bongo-net surveys of the northern Gulf of Mexico. Monthly mean was calculated by summing individual station densities and dividing by the number of stations sampled. Month was summed across years (1982–1986). Values in square brackets are total stations sampled; numbers in parenthesis next to mean densities are number of stations where larvae were collected

Taxa	Spring			Summer			Fall			
	March [144]	April [164]	May [291]	June [354]	July [139]	August [224]	September [175]	October [116]	November [110]	December [108]
Chloroscombrus chrysurus	–	–	0.2 (5)	44.5 (145)	40.0 (60)	42.9 (88)	33.6 (94)	0.3 (12)	[a](1)	–
Decapterus punctatus	[a](2)	0.2 (9)	0.2 (16)	2.3 (66)	0.3 (19)	1.5 (17)	8.2 (47)	2.9 (33)	1.1 (21)	<0.1 (4)
Trachurus lathami	1.3 (36)	<0.1 (17)	[a](9)	–	–	–	–	–	–	<0.1 (4)
Selar crumenophthalmus	–	[a](2)	[a](7)	<0.1 (14)	<0.1 (9)	0.4 (34)	0.1 (14)	0.2 (15)	0.2 (17)	–
Caranx crysos	–	[a](2)	[a](5)	0.4 (53)	1.5 (30)	0.5 (64)	[a](8)	–	–	–
C. hippos/latus	–	<0.1 (13)	0.6 (62)	0.4 (48)	0.1 (16)	[a](4)	0.1 (16)	[a](2)	–	–
Hemicaranx amblyrhynchus	–	–	–	0.2 (6)	0.1 (2)	<0.1 (2)	–	–	–	–
Seriola spp.	–	[a](8)	[a](7)	[a](4)	–	[a](3)	[a](3)	[a](3)	[a](1)	–
Selene spp.	–	–	[a](1)	0.3 (41)	0.3 (23)	0.4 (38)	0.2 (16)	[a](3)	–	–
Oligoplites saurus	–	–	–	<0.1 (5)	0.2 (4)	<0.1 (3)	–	–	–	–

[a]Mean density less than 0.05/100 m³

Results

Species distributions

Collections contained 29,203 carangid larvae from 13 species or species complexes in 11 genera. Numerically, *Chloroscombrus chrysurus* accounted for 82.9% of all larvae collected, followed by *D. punctatus* (8.8%), *Caranx hippos/latus* (2.9%), and *C. crysos* (1.9%). Other species contributed only 997 larvae or 3.5% to the numerical total. Larvae of *Chloroscombrus chrysurus* ($n = 24,218$) were abundant and widely distributed from May through November, but were most frequently collected during summer (Tables 1, 2). *C. chrysurus* were more abundant west than east of the Mississippi River delta, and relatively uncommon south of Tampa Bay, Florida (Fig. 2). Larvae were collected primarily over the inner shelf at surface water temperatures of 27°C and higher (Table 3).

D. punctatus ($n = 2,582$) was the second most frequent and abundant taxon. Round scad larvae were collected primarily off Florida during fall (Fig. 2) at stations less than 70 m deep, and at water temperatures and salinities of 25°C and 33.7 ppt or higher (Tables 1, 2, 3). Although *D.punctatus* was caught during all months sam-

pled, only four stations in December contained larvae (Table 1), all south of 27° 00′ N (i.e., below Tampa Bay, Florida) in waters more than 1,000 m deep. Larvae of *T. lathami* ($n = 240$) were collected during December and from March through May, and those of *Selar crumenophthalmus* ($n = 256$) were captured from April through November, but most frequently from August through November (Table 1). Both *T. lathami* and *S.crumenophthalmus* were taken primarily at stations deeper than 40 m; however, *T.lathami* was collected in cooler waters (median 21.4°C) than *S.crumenophthalmus* (median 28.2°C; Table 3). Most positive catch stations for *S.crumenophthalmus* were west of the Mississippi River delta and along the outer shelf. Sampling was too spatially restricted from December through February to assess adequately the gulf-wide distribution of *T. lathami* during winter, when larvae were abundant near the Mississippi River delta.

SEAMAP samples contained at least three species of *Caranx* (Fig. 3). We separated most early *Caranx* larvae into species or species complexes based on differences in pigmentation and body shape. *Caranx crysos* larvae have a series of discrete melanophores ventrally along the visceral mass and a pronounced gap in dorsal pigmentation between the nape and developing soft dorsal fin origin (Fig. 3a). Early *C. hippos/latus* and *C. bartholomaei/ruber*

Table 2 Mean density of carangid larvae (number/100 m³) for the northern Gulf of Mexico by season and region. Density by season and region was calculated by summing densities across stations and dividing by the total number of stations sampled. Numbers in parentheses are stations where larvae were collected and total stations sampled
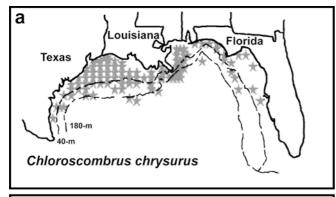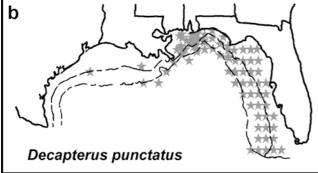
Region	Spring (March–May)	Summer (June–August)	Fall (September–November)	Regional mean
Chloroscombrus chrysurus				
Eastern	0.0 (0/139)	3.5 (19/171)	5.6 (22/109)	2.9 (41/419)
Central	0.1 (5/383)	53.9 (154/299)	10.2 (49/209)	20.5 (208/891)
Western	0.0 (0/77)	57.6 (120/247)	38.2 (36/83)	42.8 (156/407)
Season mean	< 0.1 (5/599)	43.1 (293/717)	14.7 (107/401)	
Decapterus punctatus				
Eastern	0.7 (19/139)	6.3 (70/171)	14.9 (65/109)	6.7 (154/419)
Central	[a](8/383)	0.1 (10/299)	1.3 (35/209)	0.4 (53/891)
Western	0.0 (0/77)	0.2 (22/247)	[a](1/83)	0.1 (23/407)
Season mean	0.2 (27/599)	1.6 (102/717)	4.7 (101/401)	
Trachurus lathami				
Eastern	< 0.1 (12/139)	0.0 (0/171)	0.0 (0/109)	[a](12/419)
Central	0.5 (43/383)	0.0 (0/299)	0.0 (0/209)	0.2 (43/891)
Western	< 0.1 (7/77)	0.0 (0/247)	0.0 (0/83)	[a](7/407)
Season mean	0.3 (62/599)	0.0 (0/717)	0.0 (0/401)	
Selar crumenophthalmus				
Eastern	[a](2/139)	0.2 (9/171)	0.2 (15/109)	0.1 (26/419)
Central	[b](2/383)	0.1 (12/299)	0.2 (24/209)	< 0.1 (38/891)
Western	[a](5/77)	0.3 (36/247)	0.2 (7/83)	0.2 (48/407)
Season mean	[a](9/599)	0.2 (57/717)	0.2 (46/401)	
Caranx crysos				
Eastern	[a](2/139)	[a](7/171)	[a](4/109)	[a](13/419)
Central	[a](5/383)	0.3 (62/299)	[a](3/209)	0.1 (70/891)
Western	0.0 (0/77)	1.4 (78/247)	[a](1/83)	0.9 (79/407)
Season mean	[a](7/599)	0.6 (147/717)	[a](8/401)	
C. hippos/latus				
Eastern	0.2 (20/139)	[a](3/171)	[a](4/109)	< 0.1 (27/419)
Central	0.3 (31/383)	0.3 (27/299)	0.1 (12/209)	0.2 (70/891)
Western	0.7 (24/77)	0.3 (38/247)	[a](2/83)	0.3 (64/407)
Season mean	0.3 (75/599)	0.2 (68/717)	< 0.1 (18/401)	
Selene spp.				
Eastern	0.0 (0/139)	[a](4/171)	[b](1/109)	[a](5/419)
Central	0.0 (0/383)	0.3 (39/299)	< 0.1 (11/209)	0.1 (50/891)
Western	[b](1/77)	0.6 (59/247)	0.3 (7/83)	0.4 (67/407)
Season mean	[b](1/599)	0.3 (102/717)	0.1 (19/401)	

[a]Mean density less than 0.05/100 m³
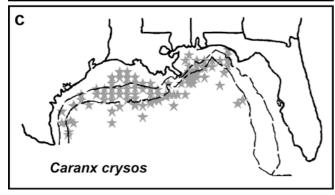
[b]Mean density less than 0.005/100 m³

Fig. 2a–c Distribution of the larvae of three species of carangid collected during Southeast Area Monitoring and Assessment Program bongo-net surveys of the northern Gulf of Mexico (1982 through 1986). Plots are for the month or season of greatest abundance (i.e., August for *Chloroscombrus chrysurus*; fall for *Decapterus punctatus*; and August for *Caranx crysos*)

larvae have a nearly contiguous series of melanophores ventrally along the visceral mass and dorsally along the trunk (Fig. 3d, h). Early *C.bartholomaei/ruber* larvae, however, have a 'deflected' dorsolateral row of pigments that runs diagonally across the trunk and pigment ventrally along the caudal peduncle that *C.hippos/latus* lack (Fig. 3d, h). Early larvae of *C.bartholomaei/ruber* also have a series of trunk melanophores along the lateral midline that extends from just behind the head to the caudal peduncle. This same lateral midline series begins behind the anus in *C. hippos/latus* larvae (Fig. 3d, e, h). After notochord flexion, the body profile of *C. hippos/latus* and *C.bartholomaei/ruber* becomes deeper and more rounded than in *C. crysos* of comparable length (Fig. 3).

Larvae of *C. hippos/latus* ($n = 848$) and *C. crysos* ($n = 558$) had similar spatial, but different temporal distributions. While both taxa were more abundant west than east of the Mississippi River delta and over the outer continental shelf, *C. hippos/latus* was collected primarily during May and June at 33 ppt and higher, and *C. crysos* was collected primarily from June to August at less than 33 ppt (Tables 1, 3). Both *C. hippos/latus* and *C. crysos* exhibited diel catch differences that favored higher catches during the day ($P = 0.001$ and $P = 0.002$, respectively). SEAMAP samples contained only six larvae of *C. bartholomaei/ruber* (3.5–5.5 mm), all caught during May 1982 at three stations 3,148 m deep near 26° 00′ N, 87° 05′ W (Fig. 4).

The larvae of other carangid species were relatively uncommon. *Selene* spp. ($n = 329$) larvae were most abundant during summer over the outer continental shelf and west of the Mississippi River delta (Tables 1, 2, 3). Early bluntnose jack larvae (*Hemicaranx amblyrhynchus*; $n = 64$; 2.0–5.3 mm SL) were collected at only 10 of 717 stations sampled during summer. All positive catch stations were located along the Louisiana/Texas inner shelf in waters less than 26 m deep (nearly all during June at a salinity of 32 ppt; Tables 1, 3; Fig. 4). We found that pigment on the roof of the mouth and the bilateral and dorsal midline rows of pigment separated *H. amblyrhynchus* larvae (Fig. 5) from those of other co-occurring species. Larvae of *Oligoplites*

Table 3 Environmental data for stations where larvae were collected during SEAMAP bongo-net surveys (1982–1986) of the northern Gulf of Mexico. Differences in the total number of stations sampled between parameters result from missing data. Data were combined across seasons, regions, depth zones, and years

Species	Number of positive stations	Median salinity (ppt)	Salinity range (ppt)	Number of positive stations	Median temperature (°C)	Temperature range (°C)	Number of positive stations	Median station depth (m)	Depth range (m)
Chloroscombrus chrysurus	384	29.8	10.4–36.6	393	29.0	22.7–33.0	405	21	4–651
Decapterus punctatus	203	35.2	17.2–37.1	223	27.9	19.0–33.3	230	40	8–3,347
Trachurus lathami	29	36.2	9.2–37.7	59	21.4	14.3–27.6	62	84	16–3,475
Selar crumenophthalmus	107	35.3	18.9–37.4	108	28.2	21.0–31.1	112	70	11–3,219
Caranx crysos	157	33.1	23.4–36.7	158	29.0	24.1–33.8	162	80	9–3,148
C. hippos/latus	136	35.8	13.4–38.1	158	27.4	22.7–32.2	161	395	9–3,413
Hemicaranx amblyrhynchus	10	30.9	24.8–33.0	9	28.6	27.0–29.4	10	12	8–26
Seriola spp.	22	36.1	18.7–37.8	28	26.9	21.3–29.6	29	208	18–3,203
Selene spp.	118	32.3	13.4–36.6	119	28.9	23.5–30.9	122	50	7–1,793
Oligoplites saurus	12	31.9	20.2–36.0	2	29.2	27.8–32.0	12	17	11–59

Fig. 3 Early larvae of *C. crysos* and two *Caranx* complexes collected during SEAMAP bongo-net surveys of the northern Gulf of Mexico from 1982 through 1986: *Caranx crysos*: **a** 3.4 mm, **b** 4.8 mm, **c** 6.8 mm; *Caranx hippos/latus*: **d** 3.6 mm, **e** 4.7 mm, **f** 7.1 mm, **g** 13.2 mm; *C. bartholomaei/ruber*: **h** 3.8 mm, **i** 5.5 mm standard length
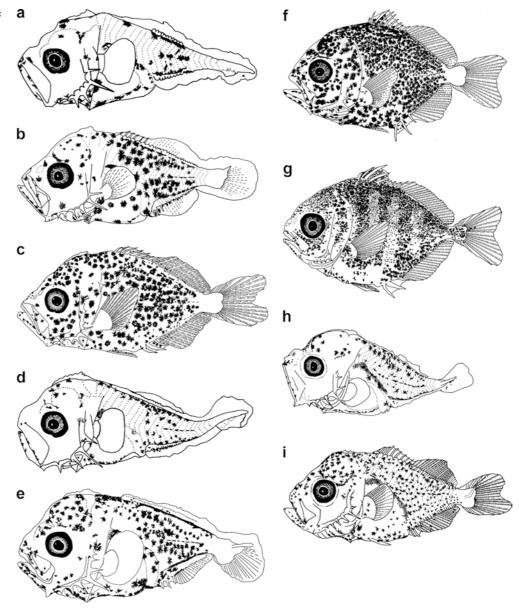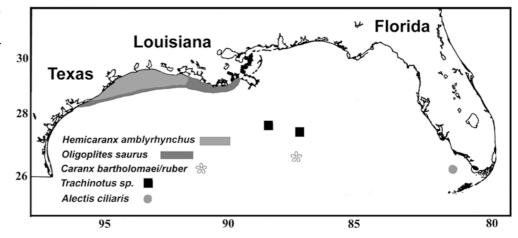
Fig. 4 Distribution of some less abundant carangids collected during SEAMAP bongo-net surveys of the northern Gulf of Mexico from 1982 through 1986. The distribution of *Oligoplites saurus* overlaps that of *Hemicaranx amblyrhynchus* in the lighter gray area

saurus (leatherjackets; $n = 54$; 1.8–5.3 mm) were collected from June through August, generally shoreward of the 20 m isobath (Fig. 4). All *Seriola* spp. larvae ($n = 48$) smaller than 5.0 mm could not be identified to species because dorsal and anal ray development was incomplete. *Seriola* larvae were widely distributed from
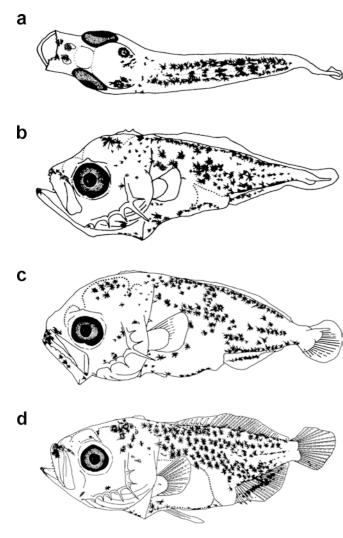
a

b

c

d

Fig. 5a–d *H. amblyrhynchus* (top to bottom 3.1 mm dorsal and lateral views, 4.0 mm, and 5.3 mm SL)

April through October and were collected primarily at stations more than 40 m deep (Tables 1, 3; Fig. 4). Samples contained two larvae of pompano (*Trachinotus* spp.) and one African pompano (*Alectis ciliaris*). Both *Trachinotus* larvae (2.2–2.3 mm) were caught during April 1984 at stations more than 1,800 m deep (Fig. 4). The only African pompano larva (7.5 mm) was collected during June 1982 off South Florida at 36.3 ppt, 28.2°C, and in waters 33 m deep (Fig. 4).

Zooplankton displacement volumes

Zooplankton displacement volumes (ZDVs) differed among regions, with distance from shore, and seasonally (Table 4). Overall, the central and western Gulf had significantly higher ZDVs than did the eastern Gulf (Table 5). ZDVs over the inner shelf (less than 40 m) tripled from winter to spring and declined thereafter, whereas volumes remained generally consistent throughout the year over the outer shelf, and in oceanic waters. Overall, ZDV was inversely related to surface salinity (canonical loading = 0.690) and station depth (canonical loading = 0.955), and positively related to surface water temperatures, but not significantly so. Differences among years were not significant.

ZDVs were consistently higher near the Mississippi River delta and along the western Louisiana/east Texas shelf, and moderately high along the shelf break during summer and fall, with localized pockets of elevated volumes over the eastern Gulf shelf (Fig. 6a–d). Similarly, ZDVs were moderately high over the shelf break during summer and fall, and also over the Florida continental shelf during fall. ZDVs were high near the Mississippi River Delta during winter (Fig. 6d).

The distribution of *D. punctatus* larvae over the continental shelf during fall and of *Chloroscombrus chrysurus* over the inner shelf during August (Fig. 2) was significantly correlated with higher ZDVs (Table 6). Despite the large number of plankton samples taken over the study period (more than 1,800 samples), *C. chrysurus* and *D. punctatus* were the only carangids abundant enough to statistically examine distribution patterns relative to areas of higher ZDVs. Nevertheless, locations along the inner shelf where larvae of *H. amblyrhynchus* and *O. saurus* were abundant during summer (Figs. 4, 6b), and near the Mississippi River delta where *Trachurus lathami* was abundant during winter and spring had higher coexisting ZDV values.

Discussion

C. chrysurus, one of the most abundant and widely distributed carangids in the Gulf of Mexico, spawn primarily during summer in waters less than 40 m

Table 4 Mean wet zooplankton displacement volumes (ml/100 ^{3}) for the northern Gulf of Mexico from SEAMAP bongo-net surveys (1982 through 1986). Mean volume was calculated by summing individual station densities and dividing by the number of stations sampled per region or depth zone. Month was summed across years

ND No data

	Spring			Summer			Fall		
	March	April	May	June	July	August	September	October	November
Region									
Eastern	11.7	9.7	11.9	36.4	15.0	27.4	18.0	24.2	20.0
Central	46.0	6.6	41.6	68.0	85.3	25.3	30.0	38.2	35.0
Western	ND	9.3	7.2	53.9	32.2	28.0	30.1	27.0	24.0
Depth zone									
< 40 m	58.2	120.0	181.6	80.1	76.8	49.9	35.6	52.4	42.5
41–180 m	35.3	27.3	20.5	22.8	14.0	22.5	15.7	16.0	14.4
> 180 m	13.8	6.3	8.0	7.2	6.2	7.7	6.4	4.8	7.6
Total stations	137	163	269	306	136	223	152	108	107

Table 5 Spatial and temporal distribution of wet zooplankton displacement volumes (ml/100 m³) for the northern Gulf of Mexico. Tukey's multiple range test established the significance of distribution patterns. Different letters within categories indicate significant differences at $\alpha = 0.05$

	Total stations	Mean volume (SD in parentheses)	Coefficient of variation	Tukey's multiple range test
Region				
Eastern	417	21 (31)	144%	C
Central	843	42 (64)	152%	A
Western	404	31 (44)	142%	B
Season				
Spring	590	26 (50)	192%	B
Summer	707	44 (63)	144%	A
Fall	367	29 (31)	108%	B
Depth				
<40 m	634	67 (73)	92%	A
40–180 m	485	21 (19)	92%	B
>180 m	545	7 (7)	97%	C

deep (Table 7). The fact that Atlantic bumper grow more quickly during summer (Leffler and Shaw 1992; Sanchez-Ramirez and Flores-Coto 1998) when water temperatures and ZDVs are traditionally high should not be surprising given that water temperature and food availability influences growth rates. The overlapping spatial and temporal distributions of higher quantities of Atlantic bumper and ZDVs suggest that the availability of food over the inner shelf during summer may have a positive affect on Atlantic bumper survival.

We found that the three species of 'scad' (*Decapterus*, *Trachurus*, and *Selar*) spawn primarily over the outer continental shelf, but utilize different spawning strategies to reduce co-occurrence of larvae. *T. lathami* are cool-water spawners (generally 22°C or lower) and are abundant in the eastern (Leak 1977), central (Ditty and Truesdale 1984), and southern Gulf of Mexico (Flores-Coto and Sanchez-Ramirez 1989) during winter/early spring when large schools of adults are present along the outer shelf (Leak 1977). In contrast, *Decapterus* and *Selar* spawn in warmer waters (generally above 24°C), with *D. punctatus* more abundant in the eastern Gulf and *S. crumenophthalmus* more abundant west of the Mississippi River delta. The fact that schools of adult *S. crumenophthalmus* (Reintjes 1979) co-occur along the outer shelf/shelf break in the western Gulf when larvae are more abundant is consistent with the possibility that this area and possibly the southern Gulf (Flores-Coto and Sanchez-Ramirez 1989) may be a spawning and nursery area for bigeye scad.

The existence of *D. punctatus* larvae south of 27° 00′ N during all months sampled in this study, when combined with similar findings year-round by Lyons (1978) and Leak (1981), is consistent with probable continual spawning and a southward offshore migration of adults during late fall–early winter (Klima 1971; Hales 1987), followed by a northward onshore return during spring. This north–south migration suggests unsuitable spawning conditions above 27° 00′ N during winter and may account for a pattern that has been interpreted as bimodal spawning in *D. punctatus*. Alternately, spawning could be continuous but appear bimodal (spring and fall) if egg and larval mortality is

higher during the middle of the spawning season (McBride et al. 2002).

The temporal distribution patterns we found for *Caranx crysos* larvae differed from those of Montolio (1976), who identified large numbers of *C. crysos* in Gulf oceanic waters during April–May, with a secondary peak during August–September. Although SEAMAP bongonet surveys from 1982 through 1986 collected 455 samples in oceanic waters during April and May, only nine samples contained *C. crysos* larvae. We suspect that some, if not most, of Montolio's larvae smaller than 5 mm are *C. hippos/latus* or possibly *C. bartholomaei/ruber* based on the distribution of larvae of these two species complexes in this study; the description by McKenney et al. (1958) of *C. crysos* larvae; and pigmentation differences between Figs. 1 and 2 in Montolio (1976).

We were unable to separate confidently *C. bartholomaei* from *C. ruber* because collections contained only six larvae, all smaller than those described previously (i.e., *C. bartholomaei* larger than 6.0 mm, *C. ruber* larger than 12.4 mm; Berry 1959). Gill raker counts along the lower limb separate juveniles and adults of *C. hippos* (22–27) from *C. latus* (16–18), and *C. bartholomaei* (18–21) from *C. ruber* (31–35) (Berry 1959). Adult *C. bartholomaei* and *C. ruber* are rare in the survey area and spawn during spring and summer in oceanic waters (Berry 1959; Nakamura 1980).

Four species of *Seriola* (*S. dumerili*, *S. fasciata*, *S. rivoliana*, and *S. zonata*) occur in the Gulf, but larvae of only the banded rudderfish (*S. zonata*) and greater amberjack (*S. dumerili*) have been described (Aprieto 1974; Masuma et al. 1990; Tachihara et al. 1993). Amberjack larvae smaller than 5 mm were taken from April through November (Table 1), although some species may spawn year-round off south Florida (Leak 1981). Reproductive data suggest that *S. dumerili* spawn during late spring/early summer (Thompson et al. 1998) and that *S. fasciata* spawn during late summer/fall. The center of *S. fasciata* distribution may be off Louisiana (Thompson and Brown 1994). Reproductive data are not available for *S. rivoliana* and *S. zonata*.

Lookdown larvae (*Selene setapinnis*) are found primarily in the western region of the Gulf during summer/

Fig. 6a–d Wet zooplankton displacement volumes (in ml/100 m^3) for the northern Gulf of Mexico from SEAMAP bongo-net surveys (1982 through 1986). Seasons were *spring* (March–May), *summer* (June–August), *fall* (September–November), and *winter* (December–February). *Border* delineates area sampled. *Codes* (ml/100 m^3) are *1* (<25), *2* (25-49), *3* (50-74), *4* (75-99), *5* (100-150), *6* (>150)
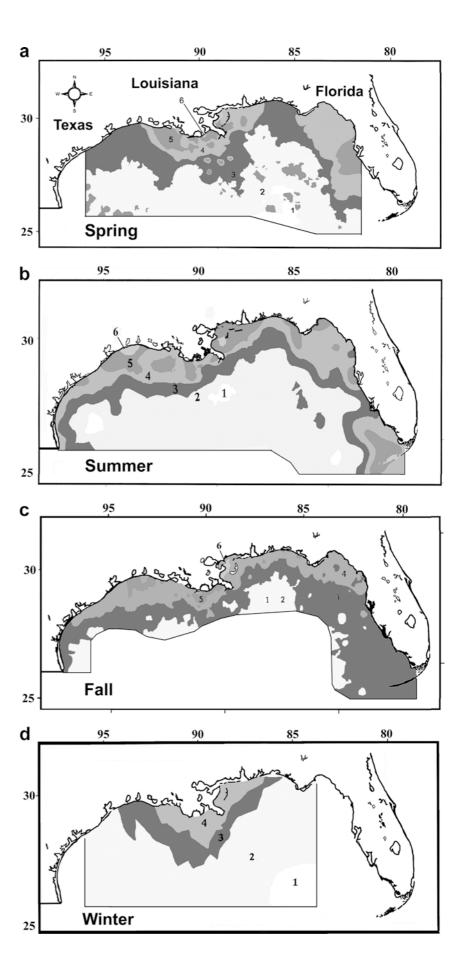
Table 6 Distribution of the larvae of two species of Carangidae from the northern Gulf of Mexico (1982–1986) relative to concentrations of zooplankton and hydrographic conditions. All stations sampled within the defined region, season, and depth zone were used in the canonical correlation analysis. Numbers in bold signify significant correlations. Correlations were 'strong' if greater than 0.70, 'moderately strong' if greater than 0.60, 'significant' if greater than 0.50, and 'weak' if less than 0.50

Taxon	Total stations sampled	Canonical R	R^2	P	Region	Season	Depth zone	Left Root	Factor structure	Right Root	Factor structure
Decapterus punctatus	109	0.564	0.318	< 0.0001	East	Fall	< 180 m	Density	–1.000	Zooplankton	**–0.797**
										Temperature	–0.315
										Salinity	0.110
										Station depth	**0.557**
Chloroscombrus chrysurus	300	0.629	0.395	< 0.0001	Central and west	Summer	< 40 m	Density	–1.000	Zooplankton	**–0.790**
										Temperature	–0.495
										Salinity	0.136
										Station depth	**0.751**

Table 7 Spatial and temporal distribution of the larvae of carangids known to occur in the northern Gulf of Mexico

Taxon	Adults[a]	Spawning season[b]				Region			Depth zone[c]			Literature cited[d]
		Spring	Summer	Fall	Winter	East	Central	West	Inner	Outer	Oceanic	
Chloroscombrus chrysurus	C		X			X	X	X	X			1, 2, 3, 4, 5, 6
Decapterus punctatus	C	?	X	X		X			X	X		1, 2, 4, 5, 7, 8, 9
Selar crumenophthalmus	C		X	X				X		X		1, 2, 4, 13, 19
Trachurus lathami	C				X	X	X	X		X		2, 3, 4, 5, 7, 10, 11, 12
Caranx hippos/latus	C	X	X				X	X	X	X		1, 4
C. crysos	C		X				X	X	X			1, 4, 5, 7, 14, 17
C. bartholomaei/ruber	R		X								X	1, 18
Seriola dumerili	C	X	X			?	X	?	?	?		20
S. fasciata	C		X	X			X		?	?		21
S. rivoliana	C	X	?			?	X	?	?	?		1
S. zonata	C	X	?		X	X				X	?	13
Hemicaranx amblyrhynchus	R		X					X	X			1, 15
Selene setapinnis	?		X	X				X		X		1, 4
S. vomer	C		X	X		?		X		X		1, 2, 4, 13
Oligoplites saurus	C	X	X						X			1, 2, 4, 13, 16, 18
Trachinotus carolinus	C	?		X	X							1, 16, 18
T. falcatus	C	?		X	X							1, 16, 18
T. goodei	R											18
Alectis ciliaris	R	X	X	?								1, 2, 10, 18
Elagatis bipinnulata	C	?	?								X	13, 18
Naucrates ductor	R	?										18, 22
Uraspis secunda	R											18

[a]*C* common, *R* rare, *?* no information
[b]*Spring* March–May, *summer* June–August, *fall* September–November, *winter* December–February
[c]Less than 40 m, 40–180 m, greater than 180 m
[d]*Literature cited*: *1* This study; *2* Leak 1981; *3* Ditty et al. 1988; *4* Flores-Coto and Sanchez-Ramirez 1989; *5* Shaw and Drullinger 1990; *6* Katsuragawa and Matsuura 1992; *7* Lyons 1978; *8* Hales 1987; *9* Montolio 1976; *10* Finucane et al. 1979a, b; *11* Ditty and Truesdale 1984; *12* Leak 1977; *13* Aprieto 1974; *14* Goodwin and Finucane 1985; *15* Hoese 1965; *16* Houde et al. 1979; *17* Klima 1971; *18* Nakamura 1980; *19* Reintjes 1979; *20* Thompson et al. 1998; *21* Thompson and Brown 1994; *22* Fahay 1975

early fall (Table 7), which is consistent with the higher reported abundance of lookdown further south off Mexico (Flores-Coto and Sanchez-Ramirez 1989; Flores-Coto et al. 2000). Although larvae of *Selene* were not particularly abundant in SEAMAP samples, larvae of the Atlantic moonfish (*S. vomer*) are common off south Florida (Aprieto 1974; Leak 1981).

The fact that *H. amblyrhynchus* larvae have only been collected along the western Louisiana/eastern Texas inner shelf (Table 7) and off Mexico (Flores-Coto et al. 1998) is consistent with the suggestion that adult bluntnose jack are uncommon in the northern Gulf (Nakamura 1980; Flores-Coto et al. 2001). Although adult *O. saurus* are common (Nakamura 1980), ichthyoplankton surveys have collected relatively few larvae. Based on our findings and other information, *O. saurus* spawn during summer over the inner shelf (Table 7).
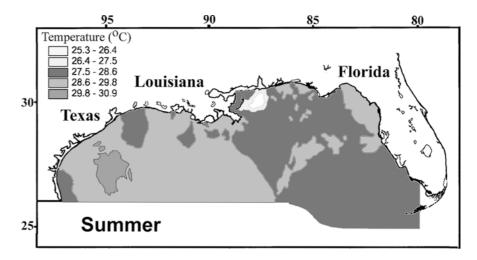
Three species of pompano (*Trachinotus carolinus*, *T. falcatus*, and *T. goodei*) occur in the study area, although bongo-net samples contained only two *Trachinotus* larvae (probably *T. carolinus*), both from oceanic waters during April. The presence of small larvae during April is consistent with a late winter/early spring spawning period for *Trachinotus* as has been suggested for United States Atlantic coast waters (Fields 1962; Fahay 1975). A proposed late winter/early spring

spawning period is also consistent with finding juvenile Florida pompano (*T.carolinus*) and permit (*T. falcatus*) relatively common during spring and summer in high-energy surf zones of the Gulf (Ruple 1984). Collection of a 5.2 mm *T.falcatus* larva during August (Flores-Coto et al. 2000) suggests summer spawning in this species. *T. goodei* (palometa) are uncommon in the northern Gulf (Nakamura 1980).

Bongo-net samples contained only one *A. ciliaris* (African pompano) larva and no larvae of *E. bipinnula-ta*(rainbow runner), *Uraspis secunda*(cottonmouth jack), or *Naucrates ductor*(pilotfish). *A. ciliaris* are apparently rare and larvae have been collected only near the southern limit of the survey area during summer and early fall (Table 7). *E. bipinnulata* spawn in oceanic waters (Aprieto 1974) and adults are common offshore, whereas adults of *U. secunda*and *N.ductor* are rare (Nakamura 1980). We found no documented record of either *U.secunda* or *N. ductor* larvae from the survey area. Fahay (1975), however, collected two young *N.ductor* smaller than 12 mm off the United States Atlantic coast during May, suggestive of early spring spawning.

We found the larvae of several species of carangids (*Chloroscombrus chrysurus*, *Trachurus lathami*,*D. punctatus*, *Caranx crysos*,*O. saurus*, and *H. amblyrhynchus*) in hydrographically dynamic areas where ZDVs are traditionally higher (Arnold 1958; Bogdanov et al. 1968; Khromov 1969; Austin and Jones 1974; Houde and Chitty 1976; Howey 1976; Dagg et al. 1987). ZDVs are consistently higher in areas influenced by riverine output as evidenced by higher volumes near and west of the Mississippi and Atchafalaya River deltas (Fig. 6), a relationship consistent with fish adapting their spawning strategy to local oceanographic conditions in order to maximize the spatial and temporal coexistence of larvae and prey (Dickey-Collas et al. 1996).

Most of the nutrient-rich freshwater discharged from the Mississippi River flows west along the shelf to form a lower salinity coastal boundary layer that extends 10–20 km from shore (Ichiye 1962; Cochrane and Kelly 1986; Wiseman et al. 1986). Over 50% of this nutrient-rich water reaches Texas (Dinnel and Wiseman 1986)

with about a 1-month lag-time (Temple et al. 1977). During late spring/early summer, southeast winds favor weak upwelling of cooler waters off Texas (Fig. 7), which triggers a reversal of coastal boundary layer flow and convergence of upwelling and riverine waters over the broad Louisiana/Texas continental shelf. As a result, lower-salinity nutrient-rich coastal waters turn offshore (Cochrane and Kelly 1986; Dagg et al. 1991), which can enhance the physical stratification of the water column and alter trophic processes [e.g., aggregation of food at intermediate trophic levels (Dagg 1988)]. Concentrations of *Chloroscombrus chrysurus* larvae over the Louisiana/ upper Texas shelf during summer (Fig. 2a) and concentrations of *T. lathami* near the Mississippi River delta during winter and early spring (Shaw and Drullinger 1990) coincide both spatially and temporally with areas of higher ZDVs (Fig. 6) and regional oceanographic processes that could enhance feeding opportunities for larvae. Similarly, concentrations of *Caranx crysos* larvae during summer at stations in a hydrographically dynamic area along the outer edge of the continental shelf (Figs. 2c, 6b) are consistent with a linkage between regional oceanographic processes (e.g., shelf mixing of riverine and coastal boundary layer waters) and biological productivity.

Based on the spatial and temporal distributions of carangid larvae in this study, the abundant but unidentified carangid near the Mississippi River delta during early fall (Grimes and Finucane 1991) may be the larvae of *C.crysos*. Similarly, concentrations of an unidentified carangid along the eastern edge of the Loop Current during spring (Richards et al. 1993) may be *D. punctatus*larvae. Concentrations of *D. punctatus* in areas where ZDVs are higher (Farris 1961; Conand and Franqueville 1973; Ortner et al. 1989; Katsuragawa and Matsuura 1992) should not be surprising given that *Decapterus, Trachurus*, and *Selar* are planktivorous throughout life.

The small number of larval *C. crysos* taken in SEAMAP and other Gulf ichthyoplankton surveys (Flores-Coto and Sanchez-Ramirez 1989; Katsuragawa and Matsuura 1992) is surprising given the abundance of adults in the survey area (Klima 1971). Similarly, the

fact that fishery surveys show juvenile and adult *T. lathami*,*E. bipinnulata*, *C.hippos/latus*, *Seriola*, and *Trachinotus* to be more abundant than ichthyoplankton surveys suggest inadequate sampling at appropriate times and locations, gear avoidance, or gear bias. Patterns of abundance vary widely with gear, mesh size, and depth sampled. In theory, oblique bongo-net tows, such as those reported here, sample the water column in an unbiased way (Kingsford 1988). Oblique tows, however, poorly represent species that primarily occupy surface waters because bongo nets under-sample narrow vertical strata. Similarly, larvae of some species may be concentrating in deeper waters or near the bottom beyond depths sampled by SEAMAP protocol.

In conclusion, co-occurrence of concentrations of larvae of some species of carangids with areas of higher ZDVs suggests that these areas serve as important nurseries. While higher total ZDVs are not a direct measure of food availability of the appropriate size and species composition (Sameoto 1984), the co-occurrence of higher concentrations of larvae and zooplankton adds to the probability of successful feeding, growth, and survival (Kingsford 1988; Grimes and Finucane 1991).

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